

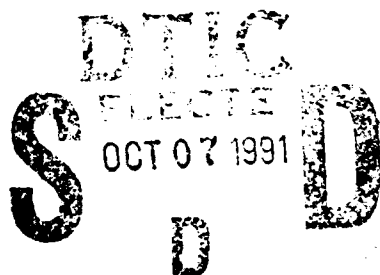


(2)

MASSACHUSETTS INSTITUTE OF TECHNOLOGY  
ARTIFICIAL INTELLIGENCE LABORATORY  
and  
CENTER FOR BIOLOGICAL INFORMATION PROCESSING  
WHITAKER COLLEGE

A.I. Memo No. 1240  
C.B.I.P. Paper No. 54

April 1990



**A Model for Rivalry between  
Cognitive Contours**

Manfred Fahle and Günther Palm<sup>1</sup>

**Abstract**

**91-12379**



The interactions between illusory and real contours have been investigated under monocular, binocular and dichoptic conditions. Results show that under all three presentation conditions, periodic alternations, generally called rivalry, occur during the perception of cognitive (or illusory) triangles, while earlier research had failed to find such rivalry (Bradley & Dumais, 1975). With line triangles, rivalry is experienced only under dichoptic conditions. A model is proposed to account for the observed phenomena.

This report describes research done within the Artificial Intelligence Laboratory and the Center for Biological Information Processing (Whitaker College) at the Massachusetts Institute of Technology E25-201 Cambridge, Massachusetts 02139, USA and at the Department of Neuroophthalmology of the University Eye Clinic in D7400 Tübingen, West Germany. Support for the A.I. Laboratory's artificial intelligence research is provided in part by the Advanced Research Projects Agency of the Department of Defense under Office of Naval Research contract N00014-85-K-0124. Support for this research is also provided by a grant from the Office of Naval Research, Engineering Psychology Division. Dr. M. Fahle holds a Heisenberg Stipend from the Deutsche Forschungsgemeinschaft (Fa 119/5-1 and Fa 119/3-2).

<sup>1</sup>Vogt-Institut für Hirnforschung, Moorenstr. 5, D4000 Düsseldorf, FRG.



## Introduction.

If different images fall upon corresponding retinal points of both eyes, for example from different objects far away from the horopter, the brain has to decide which of these two images to incorporate into the cyclopean image (Julesz, 1971; Fahle, 1982). If the two features are of similar strength they will be incorporated alternatively into the cyclopean view. Most of the time one of them will be suppressed, i.e., unavailable for conscious perception. Binocular suppression is a trick used by the visual system to overcome some of the problems caused by incomplete reconstruction of the third dimension. In the laboratory, a related phenomenon can be brought about by presenting non fusible stimuli to corresponding parts of both eyes. With prolonged presentation, perception alternates between the two stimuli — a phenomenon called binocular rivalry (Breese, 1909; Sloane, 1985; Wolfe, 1986; Grossberg, 1987; Lehky, 1988; Blake, 1989).

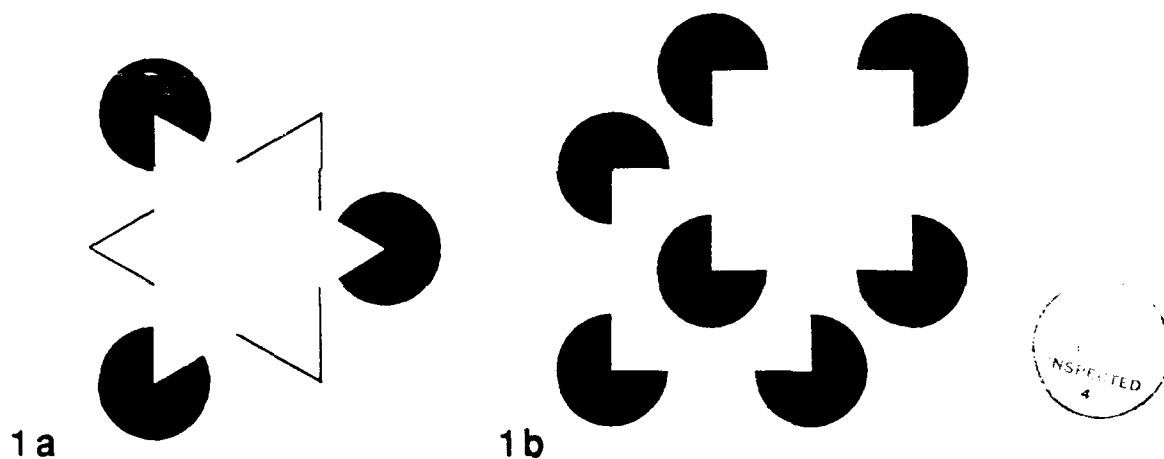


Fig. 1. Examples of cognitive contours. The shapes are only partially defined by 'real' contours but both the triangle and the squares are clearly perceived. After a) Kanizsa (1955); b) Cavanagh (1987).

Here we have studied perceptual rivalry of not only real but also illusory contours. Illusory contours are shapes which are not — or at least not all along their extent — defined by transitions in luminance, wavelength, or any other physical parameter (cf. Schuhmann, 1904; Kanizsa, 1955; Parks, 1984). Two examples of imaginary contours are shown in Fig. 1. It has been reported that the spatial interpolation which occurs in illusory contours might be achieved at a very early stage during the cortical processing of visual information. Von der

AT

Heydt et al. (1984, 1990) have shown that cells in area 18 of monkeys increase their firing rates if stimulated by purely illusory contours. We concluded that if spatial interpolation occurs at this early level, it might be possible to elicit binocular rivalry by illusory contours and to assess whether spatial interpolation occurs before or after binocular fusion.

The experiments to be described below demonstrate that monocular and binocular rivalry (or more precisely, dichoptic rivalry, since the eyes receive different stimuli) can be elicited by cognitive contours, and that the shape of the stimulus formed by the superposition exerts an important influence upon rivalry.

## Material and Methods

Stimuli usually consisted of two triangles or two rectangles, defined either by bright, continuous lines on dark background or by cognitive contours. Fig. 2 shows the elementary stimuli and the stimulus configurations in which these elementary stimuli were used.

The stimuli were constructed using a digital computer and plotted on a laser printer with a resolution of 300 dots per inch at a size of approximately 15 cm by 15 cm for the triangles. The stimuli were then photographed on high-resolution black-and-white 35 mm film (Agfa-Ortho) at a scale of around 8:1 and mounted in etched glass slide mounts. We used the negatives proper so that the contrast of the stimuli was reversed compared to the laser printer's line drawings. The stimuli were presented by means of phase-difference haploscopy (Aulhorn, 1966). This method allowed the separation of the visual stimuli to the two eyes through temporal alternation. The ray-path of the stimulus projector was interrupted by a sector disc, rotating in front of the projector, to produce a flicker frequency of 100 Hz. The duty-cycle of the disc was around 1.2, i.e., 20% longer closed than open. A second projector for the stimulus to the contralateral eye had a sector disc rotating exactly in anti-phase such that at any given time, only one projector created an image on the screen. The phase-relation between the sector discs was kept constant by use of synchronized motors locked to the line frequency. The observer, his or her head stabilized by a headrest, looked through a special pair of spectacles. These spectacles contained two sector discs rotating in anti-phase, while each of the discs of the spectacle was in phase with one of the projector's sector discs. Then.

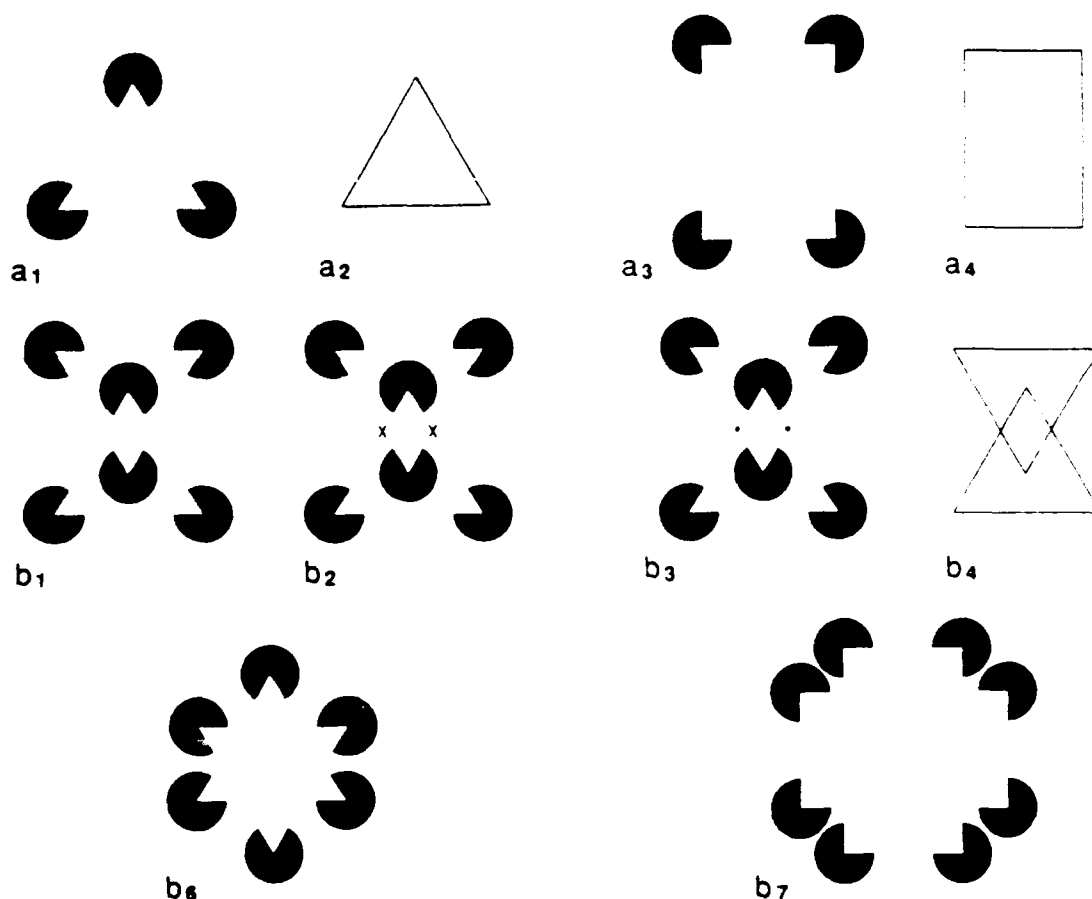


Fig. 2. Pairs of the elementary stimuli *a* (1-4) were combined to yield the stimulus-configurations *b* (1-5). *a*) *Elementary stimuli*: a triangle, defined either by cognitive contours (*a*<sub>1</sub>) or by lines (*a*<sub>2</sub>) and a rectangle, again either as a cognitive contour (*a*<sub>3</sub>) or as a line stimulus (*a*<sub>4</sub>). *b*) *Stimulus configurations*: *b*<sub>1</sub>) Two illusory triangles, rotated by 180° relative to each other, with a vertical displacement between the two of 1/3 of the triangle's height. *b*<sub>2</sub>) Same configuration as *b*<sub>1</sub>, but little crosses at the (imaginary) intersections of the cognitive contours. *b*<sub>3</sub>) Same configuration as in *b*<sub>2</sub>, but points were used instead of crosses. *b*<sub>4</sub>) Two triangles as in *b*<sub>2</sub>, but with solid lines instead of cognitive contours. *b*<sub>5</sub>) Two triangles rotated by 180°, with a vertical displacement of 1/3 stimulus height, but in the direction opposite that of configuration *b*<sub>1</sub>. *b*<sub>6</sub>) A cross consisting of two rectangles rotated by 90°.

each eye saw only the stimulus of one projector. The flicker frequency was 100 Hz, far above the flicker fusion frequency. Each motor and disc could be rotated as a whole by hand, which allowed a variation of the phase relation between the projectors and spectacles as well as between the projectors or between the two discs of the

spectacles. These manipulations determined whether the presentation was monocular, binocular (= both eyes see identical stimuli), or dichoptic (= each eye sees only one of the elementary features; e.g. one eye sees the base-up triangle of Fig. 2b<sub>4</sub> while the other eye sees the base-down triangle).

The triangles had a height of 5°, the size of the rectangles was 3.5° x 7°; they were projected at an observation distance of 2.5 m to a white screen, extending over 60° x 40° of visual angle. The luminance of the bright elements of the stimulus was around 2 cd/m<sup>2</sup>, their contrast  $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min})$  amounted to 93%. Room illumination was supplied by overhead incandescent lighting at approximately 0.1 cd/m<sup>2</sup>. In part of the experiments, a bright square with a side length of 12° was presented binocularly as a fusion aid in order to decrease vergence eye movements, especially under dichoptic conditions.

The observers looked through the spectacles and were instructed to gaze at the stimuli for a while and then to start the session by pressing briefly one of three push-buttons. The upper button signaled that the upper triangle dominated, the lower button was to be pushed as soon as the lower triangle dominated, while the middle one was to indicate that the observer saw both triangles (or rectangles) equally well.

A large intersubject variation was to be expected between the criteria used by different subjects in this task. We tried to make the criteria for different observers as similar as possible by instructing the observers to signal a dominance only if one of the stimuli had completely or at least more than half disappeared. Furthermore, no comparison between different subjects will be made, but only between different conditions for each subject. The sequence of testing of the different conditions varied between observers in a pseudo random order to prevent effects of practice from influencing the results. A computer (Atari 1040ST) registered the observer's responses and calculated the lengths of the dominance times. After three minutes, the next press of any button marked the end of the experimental run, and triggered an acoustical signal. Time intervals for each of the three perceptual classes were added separately. The number of transitions between the two 'extreme' percepts was calculated, i.e. the transitions between the percept 'upper stimulus dominates' and 'lower stimulus dominates' — irrespective of whether

the transition was direct or via 'both stimuli simultaneously perceived'. Only complete transitions between the two extremes were counted. The total dominance times and the number of transitions were normalized for a standard duration of three minutes. Two transitions — from pattern A to pattern B, and back — marked one reversal. In the graphs, the number of reversals for a three minute period is shown. The program calculated the ratio of dominance between the two stimuli, its standard error, and the ratio between dominance of a single stimulus and the times when both stimuli were perceived simultaneously.

Altogether ten observers participated in the experiments. They were volunteer students and staff of Tübingen University, and all but one (MF) were unaware of the purpose of the experiment. They were between 20 and 45 years of age. About half of them had had extensive experience with psychophysical experiments, and all had normal or corrected to normal visual acuity, and no visual disorders as revealed by standard ophthalmological tests.

## Results

All of our subjects vividly experienced rivalry between cognitive contours (though less complete than with real contours), both under dichoptic conditions and, more surprisingly, during monocular and binocular viewing. The subjective contours of the triangle of Fig. 2a<sub>1</sub> were perceived as in periodical alternation with each other when presented in the configuration of Fig. 2b<sub>1</sub> and were hardly ever perceived simultaneously. We did not find a clear subjective difference between rivalry under binocular, monocular or dichoptic conditions - apart from a tendency of the two triangles to move relative to each other horizontally in dichoptic presentations. This effect is to be expected under dichoptic conditions with non-fusable stimuli and is due to vergence eye movements. Addition of a binocularly visible bright square around the stimuli as a fusion aid decreased the amount of these movements but could not abolish them completely. The mean number of alternations within the three minute period is shown in Fig. 3 for our ten observers. Both the absolute number of alternations (Fig. 3a) and the normalized number as in Fig. 3b (where the periods during which *both* stimuli were perceived have been eliminated) showed a similar pattern of results: The number of alternations was not significantly different between binocular (Fig. 3a,b: binl) and monocular rivalry (monl) of the

cognitive contours. The number of alternations was, however, lower under dichoptic (dich1) than under monocular or binocular conditions — probably at least partly due to the apparent movement of the stimuli under dichoptic conditions that rendered the stimuli out of alignment during part of the presentation time. The ratio of dominance between the perception times of the two stimuli was usually around 1, i.e., both triangles or squares were perceived for similar periods of time. The vergence eye movements mentioned above, leading to a sideward displacement of the stimuli, are the probable cause for the relatively slow rate of rivalry with the real triangles of Fig. 2 b<sub>4</sub> as compared to gratings of different orientations in both eyes. Such gratings yielded almost 30 reversals within the 3 minute period (Fig. 3: dich7).

Basically the same results were obtained when additional crosses, i.e., two short line segments intersecting at an angle corresponding to the intersection of the cognitive contours (Fig. 2b<sub>2</sub>) were presented at the (imaginary) intersections of the cognitive contours (Fig. 3: mon2 for monocular, bin2 for binocular viewing). The same holds true for the addition of small points instead of crosses (Fig. 3: mon3 for monocular, bin3 for binocular viewing); we found no indication for a halt in rivalry due to fusion in these stimuli.

Triangles formed by continuous lines (as in Fig. 2b<sub>4</sub>), when presented dichoptically, alternated in a similar way, but again seemed to move relative to each other (Fig. 3a: dich4). If the number of reversals was normalized by subtracting those periods when both stimuli were simultaneously perceived, the alternation rates of dichoptically presented cognitive and real contours were virtually identical (Fig. 3b: dich4). As a control, two 5° \* 5° patches of high contrast square wave gratings of 4 cycles/° were presented dichoptically with grating orientation vertical for the right eye and horizontal for the left eye (Fig. 3a,b : dich7; 'gratings'). Here, vergence movements played a much smaller role and the patterns usually did not separate spatially. Two observers who did not experience rivalry with the dichoptic real triangles and who had been excluded from condition dich6, experienced vivid rivalry with the gratings, and the average number of alternations increased in comparison to the dichoptic triangles (Fig. 3a,b: dich4-dich7). Subjectively, rivalry differed between line stimuli and cognitive contours in that, as with the monocularly or binocularly presented cognitive contours, none of the triangles disappeared completely, but one seemed to lie above the other, with the depth relation alternating.



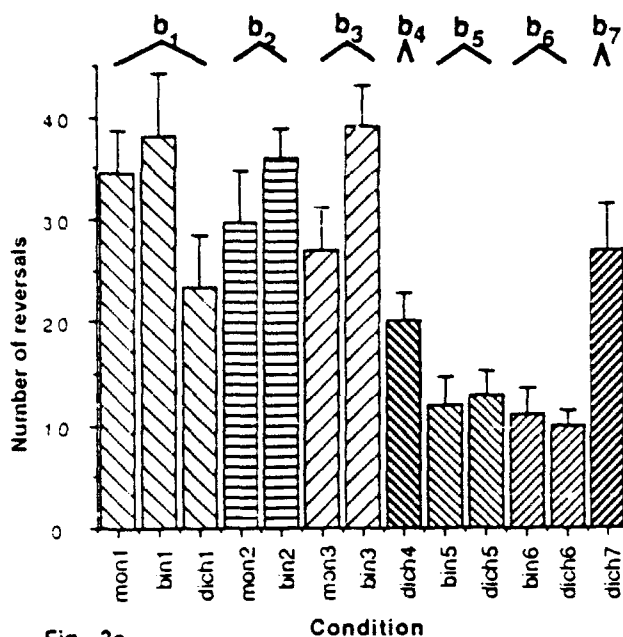


Fig. 3a

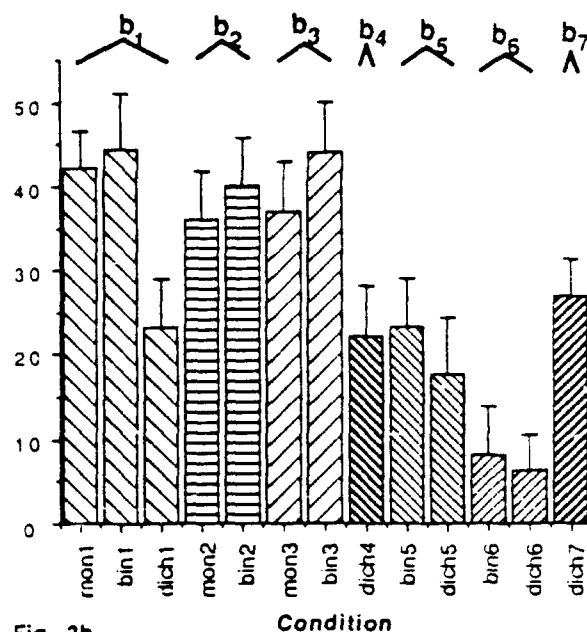


Fig. 3b

Fig. 3. Number of alternations between the perceptions of the two triangles or squares for different stimulus configurations as shown in Fig. 2. Presentation was either monocular, binocular or dichoptic. a) Raw data; b) Data compensated for times without rivalry (both stimuli perceived). For further explanations, see text. Means and standard deviations of ten observers.

With other stimulus configurations, far fewer alternations between the cognitive contours were experienced. Take as an example the star-like contour in Fig. 2b<sub>5</sub> which evolves from the strongly rivalrous stimulus shown in Fig. 2b<sub>1</sub> if one of the illusory triangles is shifted vertically by two thirds of its height. This stimulus appeared relatively stable, with fewer reversals under monocular and binocular (Fig. 3: bin5), as well as under dichoptic (dich5) conditions. The same is true for the cross-like shape in Fig. 2b<sub>6</sub> which consists of two imaginary rectangles (Fig. 3: bin6 & dich6). Some observers could perceive the outlines of this cross over extended times, without any alternations or signs of rivalry. But, upon closer inspection, one realized indications for inhibition and rivalry in these stimuli, too. The rivalry took place, of course, at the intersections of the illusory

lines. These, however, were not so crucial for the shape or the 'Gestalt' of the target in the case of the 'star' and 'cross' as they were for the target of Fig 2b<sub>1</sub>, and therefore, less rivalry with fewer alternations was experienced.

In addition to the frequency of alternation, the ratio between suppression and non-suppression times was calculated, i.e., the ratio of times when only one of the stimuli was perceived to when both were perceived simultaneously. Here again, a clear difference appeared between the different configurations (Fig. 4). Generally, the configurations allowing longer periods of simultaneous perception of both stimuli also showed fewer rivalry-alternations, even if the periods of simultaneous perception were compensated for.

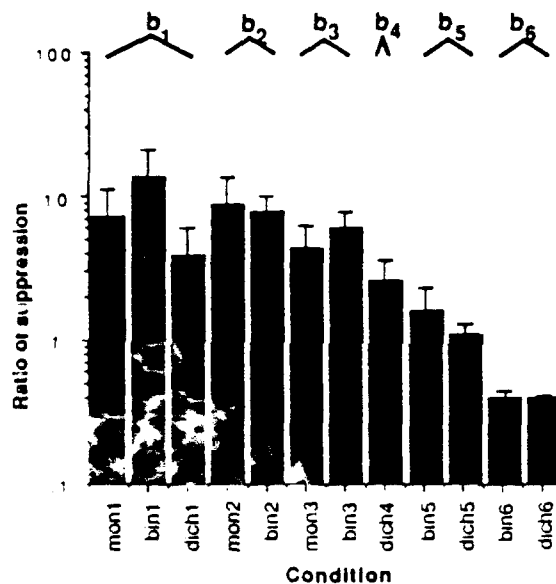


Fig. 4. Ratio between the times when one stimulus was suppressed versus when both stimuli were simultaneously perceived. The higher this ratio, the stronger the suppression.

## Discussion

There are generally two lines of explanation for psychophysical experiments or effects like the one presented here: structural and functional explanations.

Many effects can be correctly predicted and easily understood by means of the functional argument. One simply tries to imagine what real physical situation the artificial stimulus corresponds to. In most cases, perception chooses the correct physical interpretation of an

ambiguous stimulus — the brain has built-in knowledge about the world (e.g., Barlow, 1972; Marr, 1982).

But there are cases where this functional kind of explanation does not work at all, i.e., the percept deviates from the stimulus in a way that seems not to be evolutionarily advantageous, as, for example, with the flicker-induced colours (Benham, 1894) and the Hermann-Hering grid (Hermann, 1870). It is in such cases that one can assume the existence of an unwanted side-effect in the perceptual system, rather than a hidden functional explanation, and one might resort to a structural explanation. In such cases especially, one can hope to gain insight into the structure or the mechanisms of the visual system, since they can be expected to relate directly to the specific anatomy and physiology of the visual system. One could argue that a specific perceptual task can be achieved by a large number of different neuronal networks, but that the side effects (which cannot be understood functionally) give a more direct insight in the kind of neuronal operations actually performed.

A good example of such an effect on the cortical level is binocular rivalry, a side effect of the binocular inhibition required in the formation of the pseudo three-dimensional reconstruction of the visual world, as discussed in the introduction. The rivalry cannot be retinal since it involves the interaction of (conflicting) information from both eyes (cf. Blake & Overton, 1979). There seems to be no straightforward functional explanation for it: binocular rivalry does not help the visual system to increase the amount of information regarding the visual world, but seems to be a sideeffect caused by the structure of the visual system. The best explanation for the phenomenon of binocular rivalry seems to be a structural one, i.e. of an inhibition between visual cortical cells preferring incompatible orientations, colours or other elementary features in roughly corresponding retinal locations of the two eyes (cf. Logothetis & Schall, 1989). This explanation fits well with the physiological findings of lateral intracortical connections (e.g., Gilbert 1988; Gray et al., 1989). It also can be regarded as a special example of the more general idea that incompatibility of the information represented or signalled by two neurons should be implemented neurally as inhibition between these neurons, whereas supporting information should be implemented neurally as excitation.

By means of this simple principle one can provide structural explanations (and thus physiological predictions) for some of the

amazing phenomena that appear in the working of our visual system. For example, one would expect that a neuron signalling a short oriented edge should excite other neurons signalling the same orientation along the prolongation of this edge (as edges often are longer than receptive fields), whereas it should inhibit (possibly indirectly) neurons that signal incompatible orientations. Thus, a neuron which responds maximally to an oriented edge at a certain location in the visual field may also be excited by neurons responding to edges of the same orientation in neighbouring locations (along the same edge). It may also respond therefore to stimuli outside its direct receptive field, or, in other words, it may respond to cognitive contours (cf., however, Harris & Gregory, 1973; Gregory & Harris, 1974; also Ullman, 1976). Von der Heydt, Peterhans, and Baumgärtner (1984) have indeed observed neurons in area 18 of the monkey that showed such responses. Redies, Crook, and Creutzfeldt (1986) found similar neurones in cats' area 17, and cats have been shown to 'see' subjective contours (Bravo, Blake & Morrison, 1988). By the same token, the neurons signalling visual or cognitive contours of different orientations should inhibit each other, and thus we should observe binocular rivalry between differently oriented contours in corresponding locations of both eyes, be they real or illusory. Our experiment shows that we do.

The structural explanation given above appears to be the simplest for this psychophysical phenomenon. Our results agree with the results of Harris and Gregory (1973), but seem to contradict those of Bradley & Dumais (1975) and especially Bradley (1982) who found only very weak rivalry between cognitive contours. ("Dichoptic presentation of subjective contours differing in orientation does not result in binocular rivalry or contralateral suppression of the contours." Bradley, 1982). The reason for the contradiction is that Bradley and Dumais used only cognitive contours similar to our Fig. 2b<sub>1</sub>. This way, they were led to believe that cognitive contours are unable to elicit perceptual rivalry. Our results can be seen in line with a number of psychophysical investigations demonstrating that cognitive contours can interact with stereoscopic depth perception (Lawson et al., 1974; Lawson & Gulick, 1967; Harris & Gregory, 1973; Gregory & Harris, 1974; Whitmore, Lawson & Kozora, 1976; Ramachandran & Cavanagh, 1985; Mather, 1989), elicit an impression of motion (Petersik, Hicks & Pantle, 1978), elicit a tilt aftereffect (Smith & Over, 1975; cf. also Paradiso, Shimojo & Nakayama, 1989), induce a contour-attraction effect in the Bourdon illusion that is stronger than with real contours (Walker & Shank, 1988), and

transfer an aftereffect to a real contour in the Poggendorff illusion (Becket, 1989).

Unfortunately, we could not resist looking at Figure 2b<sub>1</sub> also binocularly. It turns out that the phenomenon of rivalry appears not only in dichoptic presentation, but also in binocular and monocular presentation of Fig. 2b<sub>1</sub>. At first sight, this might be interpreted as rivalry on a higher level: the two illusory triangles cannot be seen at the same time since they overlap and can only appear as a whole. Physically, it would be always one white triangle in front of the other one whose complete view is thereby prevented. And since both triangles physically have exactly the same likelihood of being on top, our visual system does not decide definitely, but shows the two possible interpretations alternately. (Cavanagh (1987) presented a very similar, but stable arrangement of subjective contours: by omitting one of the corners of the 'lower' square, the upper square was made dominant permanently (Fig. 1b)). But would it not be even better, functionally, if our visual system would show us the two white triangles at the same time, as in effect it does when the same two triangles are outlined? Furthermore, the phenomenon of rivalry does not appear to be qualitatively different, whether we display the two illusory triangles dichoptically or otherwise. And it appears to be qualitatively similar to the usual rivalry obtained with dichoptic presentation of two outlined triangles — though a direct comparison of the alternation rates was difficult due to the strong vergence eye movements experienced with the real triangles.

For these reasons, we still hold on to the structural explanation given above — the more so because it can also explain the other effects just mentioned. One has first to assume that the inhibition between different orientations appears not just between neurons preferably responding to opposite eyes, but also between the more frequent binocular neurons. Secondly, one has to assume that the inhibition is not strong enough to inhibit a neuron that receives its optimal or near-optimal sensory input. In this case the inhibition would not be strong enough to produce rivalry if both triangles are really present either binocularly or monocularly. It would be strong enough in a dichoptic presentation of real triangles, because then each triangle gets support from only one eye, while it is inhibited from both binocular neurons (that are submaximally activated) and from neurons preferring the opposite eye. And the inhibition would also be strong enough for illusory triangles in either presentation, because in this case (almost) all the crucial neurons will be far from maximally activated.

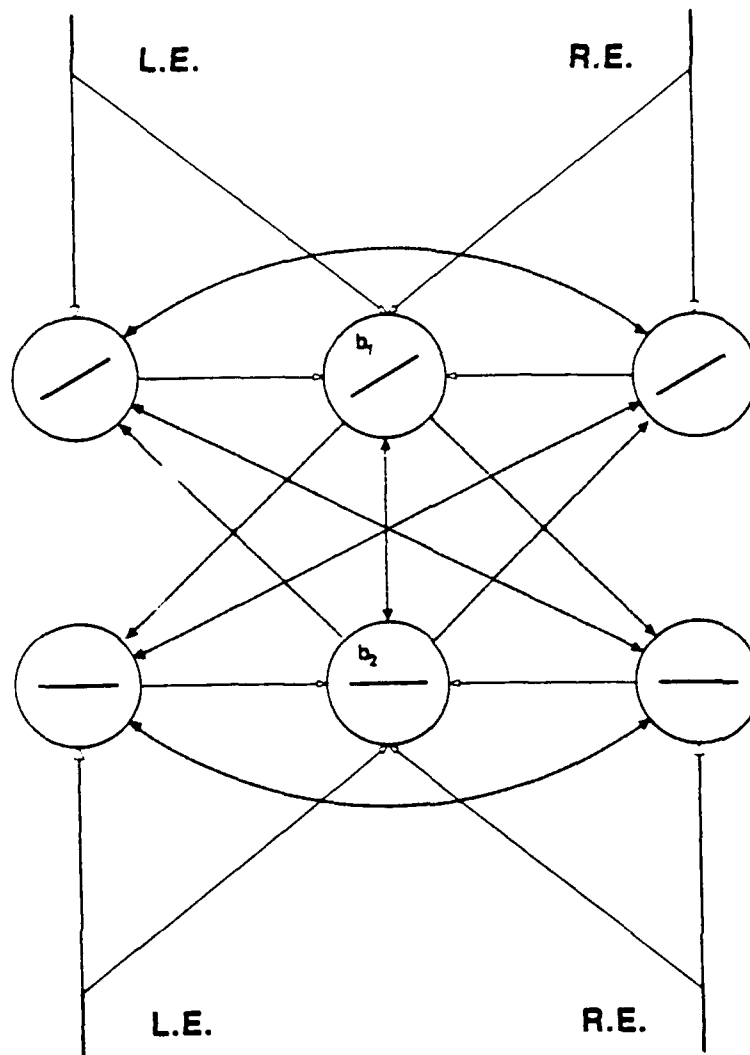


Fig. 5. A model for the explanation of rivalrous perception between real and illusory contours. The inputs of both eyes (R.E. ; L.E.) feed into orientation selective neuron pools of the visual cortex, symbolized by circles. For the sake of simplicity, only the pools for two different preferred orientations are shown. The inputs feed into both monocular pools (right and left sides) and binocular pools ( $b_1$ ,  $b_2$ ; in the center). The inputs are strong when stimulation is through real contours (2.6 relative units) and weak from cognitive contours (1.3 r.u.). Heavy lines symbolize strong interactions (1.0 r.u.); thin lines symbolize weak interactions (0.5 r.u.). Solid lines with white arrowheads are for excitatory interactions; broken lines with black arrowheads stand for inhibitory interactions. The six pools were modelled as low-pass integrators with a time constant of 6 time units, followed by a nonlinearity:  $f(x) = 1 / (1 + \exp(1/2 - 5x))$ . In addition, the pools are subject to a low pass temporal habituation with a time constant of 120 time-units.

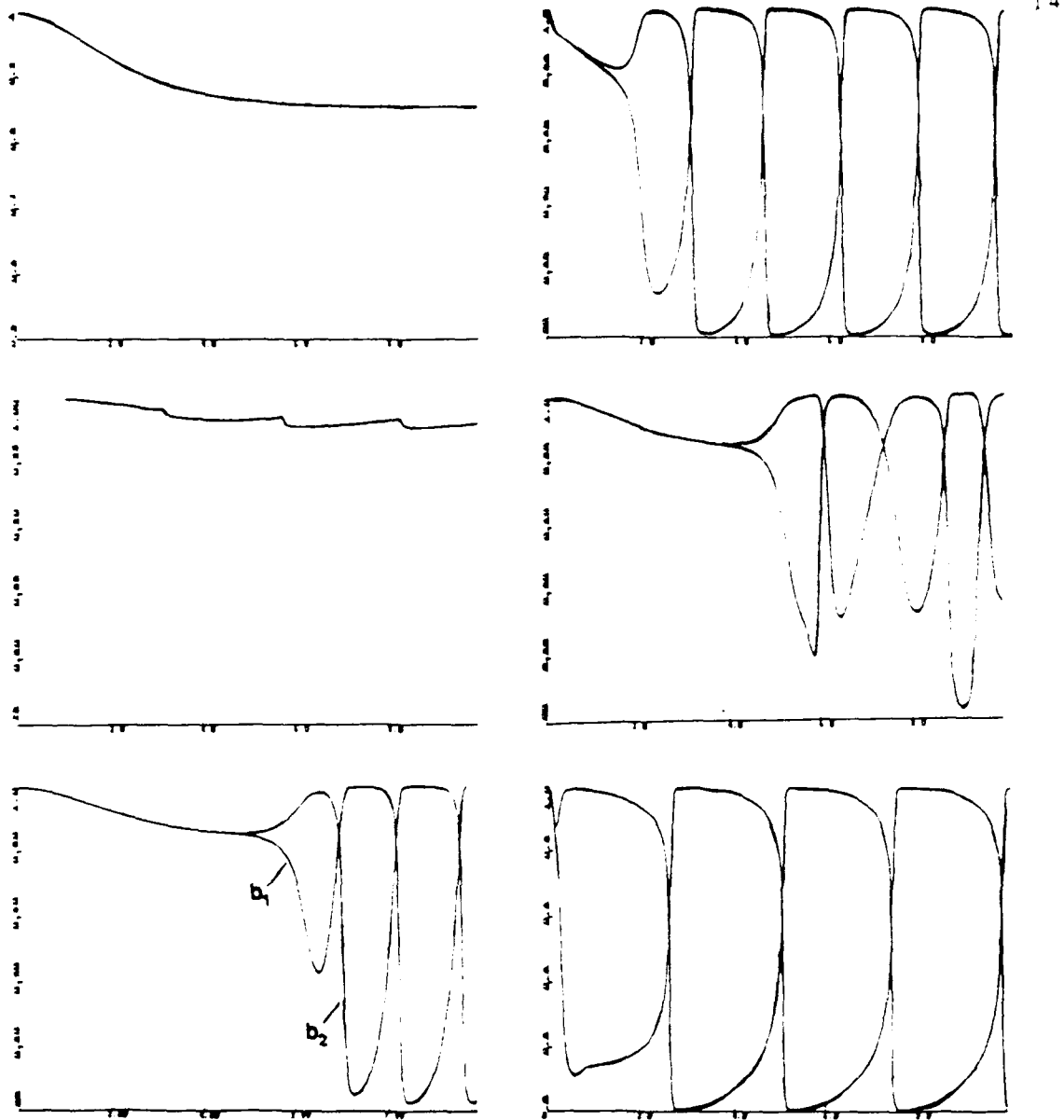


Fig. 6. Output of the model of Fig. 5 for different inputs. The abscissa denotes time in arbitrary units, the ordinate indicates the activation of the binocular neuron pools corresponding to the two orientations ( $b_1$ ,  $b_2$ ; from Fig. 5). The curves for both pools are superimposed in each of the graphs. At any one time, the pool with the higher activation dominates, and dominance alternates between the two pools, indicating perceptual rivalry. The left column shows results for 'real' line stimuli, the right column for imaginary contours. The upper row is for monocular, the middle row for binocular, and the lower row for dichoptic conditions. With monocular and binocular real line stimuli, the model does not produce rivalry and the activation of both pools is identical, well in line with subjective perception. In this simple deterministic model, one has to break the symmetry between the two sets of pools (corresponding to the different orientations) to obtain the oscillatory behaviour. We did this by choosing slightly different initial conditions in the two binocular pools.

This explanation of our experimental findings is supported by a simulation of six pools of neurons representing monocular and binocular neurons tuned to one of two incompatible orientations that are present at an intersection of the two triangles. The interaction between these six pools is as described above; it is shown in detail in Fig. 5. The illusory contours are modelled by a weaker sensory input to the corresponding pools of neurons. With this simple model, we can reproduce qualitatively the rivalry observed with our real and illusory stimuli under dichoptic, binocular, and monocular conditions. It should be stressed, however, that the model does not aim to reproducing *all* results on (binocular) rivalry that may be found in the literature, but rather illustrates that the same neuronal mechanism can account for the rivalry of both cognitive and real contours. The results of the simulations are shown in Fig. 6, which displays the activity in the binocular neuron-pools for the two orientations under the different stimulus conditions. The model correctly simulates the rivalry between cognitive contours and between real contours under the different conditions of our experiment. In addition, it is in agreement with other features of the rivalry process, e.g., dominance times of the stimuli depending directly upon the strength of the stimulus and hardly at all upon the strength of the rival stimulus.

If one slightly shifts one of the triangles in Fig. 2b<sub>1</sub>, one can achieve a star-like arrangement with six intersections of the two triangles (Fig. 2b<sub>4</sub>). This figure does not produce significant rivalry, even upon dichoptic presentation. Again, one may be tempted to explain this phenomenon as 'high-level', namely as the appearance of another 'Gestalt', the 'star' that prevents rivalry. But there is also a structural explanation on a much lower level that requires nothing more than the mechanisms discussed so far: Since each edge of each triangle is intersected twice, there is no support for the edge detectors between the two intersections, and thus they are not activated. Accordingly, one can extrapolate the illusory contours of the two triangles at most up to these intersections, and this is consistent with the appearance of a star. A similar explanation can also be given for the 'cross'.

In summary, our experiments are consistent with, and in effect lend further evidence to the hypothesis that edge detecting neurons in the visual cortex interact positively (excitatorily) along the prolongation of their edges, and negatively (inhibitorily) towards 'conflicting edges', i.e. edges that would intersect the edge being signalled by the neuron too close to its receptive field position at too large an angle. This observation encourages the more general view, that conflicting



information is implemented neurally as inhibition between the neurons signalling this information, whereas supporting information is implemented neurally by the corresponding excitation.

## Appendix

The following is a listing of the program that was used to produce the simulations of the model of Fig. 5. and which are shown in Fig. 6.

```

var
t,tau,t1,tal,d1,p0,p1,p2,p3,p4,p5,p6,p7,p8,p9,p10,a0,a1,b0,b1: real;
monol0,monol1,monor0,monor1,hplus: real;
u,d,h,a: array[0..1,1..3] of real;
sa: array[0..1] of real;
i,j,k: integer;
akt0,akt1,bin0,bin1: text;

function f(x: real): real;
begin
f:=1/(1+exp(-(5*x-0.5)));
end;

begin
assign (akt0,'akt0.sim');
assign (akt1,'akt1.sim');
assign (bin0,'bin0.sim');
assign (bin1,'bin1.sim');
rewrite (akt1);
rewrite (akt0);
rewrite (bin1);
rewrite (bin0);

{inputs}
monol0:=2.5;           {1.3 1.3 1.3 2.6 2.6 2.6}
monol1:=0.0;           {1.3 1.3 0   2.6 2.6 0}
monor0:=0.0;           {0   1.3 0   0   2.6 0}
monor1:=3.2;           {0   1.3 1.3 0   2.6 2.6}
p0:=0.5;

u[0,1]:=monol0;
u[0,2]:=(monol0+monor0)*p0;
u[0,3]:=monor0;
u[1,1]:=monor1;
u[1,2]:=(monor1+monol1)*p0;
u[1,3]:=monol1;

{initial values}
for i:=0 to 1 do
  for j:=1 to 3 do
    begin
      d[i,j]:=1;
      h[i,j]:=0;
      a[i,j]:=0;
    end;

{small asymmetry of initial values}
d[0,2]:=1.2;
d[1,1]:=1.1;

```

```

(parameters)
tau:=6;
t:=120;
ta1:=1-tau;
t1:=1-t;
p1:=0.5;
p2:=0.;
p3:=-0.5;
p4:=0.5;
p5:=1.;
p6:=0.667;
p7:=1;
p8:=1;
p9:=0.;
p10:=1.;

For k:=1 to 1600 do
begin
for i:=0 to 1 do
sa[i]:=a[i,1]+a[i,2]+a[i,3];
for i:=0 to 1 do
for j:=1 to 3 do
begin
d1:=-ta1*d[i,j]+u[i,j]+p1*a[i,j]-sa[1-i]*p2;
if (j=2) then d1:=d1+a[i,j]*p3+sa[i]*p4-p9
else d1:=d1-a[1-i,j]*p5-a[i,4-j]*p10;
d1:=d1-a[1-i,2]*p8;
d[i,j]:=d1/tau;
end;
for i:=0 to 1 do
for j:=1 to 3 do
begin
h[i,j]:=(-t1*h[i,j]+d[i,j])/t;
if (h[i,j]>0) then hplus:=h[i,j] else hplus:=0;
a[i,j]:=f(p7*d[i,j]-p6*hplus);
end;
a0:=sa[0];
a1:=sa[1];
b0:=a[0,2];
b1:=a[1,2];
writeln (a0,a1,b0,b1);
writeln (akt0,k/100.0,a0);
writeln (akt1,k/100.0,a1);
writeln (bin0,k/100.0,b0);
writeln (bin1,k/100.0,b1);
end;

close(akt0);
close(akt1);
close(bin0);
close(bin1);
end.

```

## References

Aulhorn, E. (1966) Phasendifferenz- Haploskopie. Eine neue Methode zur Trennung der Seheindrücke beider Augen. *Klin. Mbl. Augenh.* **148**, 540-544.

Barlow, H.B. (1972) Single units and sensation: a neuron doctrine for perceptual psychology? *Perception* **1**, 371-394.

Beckett, P.A. (1989) Illusion decrement and transfer of illusion decrement in real- and subjective-contour Poggendorff figures. *Perception & Psychophysics* **45**, 550-556 (1989).

Benham, C.E. (1894) Notes. *Nature* **51**, 113-114.

Blake, R. (1989) A neural theory of binocular rivalry. *Psychol. Rev.* **96**, 145-167.

Blake, R. & Overton, R. (1979) The site of binocular rivalry suppression. *Perception* **8**, 143-152.

Bradley, D.R. (1982) Binocular rivalry of real vs. subjective contours. *Perception & Psychophysics* **32**, 85-87.

Bradley, D.R. & Dumais, S.T. (1975) Ambiguous cognitive contours. *Nature* **257**, 582-584.

Bravo, M., Blake, R. & Morrison, S. (1988) Cats see subjective contours. *Vision Res.* **28**, 861-865.

Breese, B.B. (1909) Binocular rivalry. *Psychol. Rev.* **16**, 410-415.

Cavanagh, P. (1987) Reconstructing the third dimension: Interactions between colour, texture, motion, binocular disparity, and shape. *Computer Vision, Graphics, Image Proc.* **37**, 171-195.

Fahle, M. (1982) Binocular rivalry: Suppression depends on orientation and spatial frequency. *Vision Res.* **22**, 787-800.

Gilbert, C.D. (1988) Neuronal and synaptic organization in cortex. Group report in: P. Rakic & W. Singer (Eds.) *Neurobiology of neocortex*. Wiley: New York (pp 219-241).

- Gray, C.M., König, P., Engel, A.K. & Singer, W. (1989) Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature* **338**, 334-337.
- Gregory, R.L. & Harris, J.P. (1974) Illusory contours and stereo depth. *Perception & Psychophysics* **15**, 411-416.
- Grossberg, S. (1987) Cortical dynamics of three-dimensional form, color and brightness perception: 2. Binocular theory. *Perception & Psychophysics* **41**, 117-158.
- Harris, J.P. & Gregory, R.L. (1973) Fusion and rivalry of illusory contours. *Perception* **2**, 235-247.
- Hermann, L. (1870) Eine Erscheinung simultanen Kontrastes. *Pfluegers Archiv ges. Physiol.* **3**, 13-15.
- Julesz, B. (1971) *Foundations of cyclopean perception*. University of Chicago Press.
- Kanizsa, G. (1955) Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista di Psicologia* **49**, 17-30.
- Lawson, R.B., Cowan, E., Gibbs, T.D. & Whitmore, C.G. (1974) Stereoscopic enhancement and erasure of subjective contours. *J. Exp. Psychol.* **103**, 1142-1146.
- Lawson, R.B. & Gulick, W.L. (1967) Stereopsis and anomalous contour. *Vision Res.* **7**, 271-297.
- Lehky, S.R. (1988) An astable multivibrator model of binocular rivalry. *Perception* **17**, 215-228.
- Logothetis, N.K. & Schall, J.D. (1989) Neuronal correlates of subjective visual perception. *Science* **245**, 761-763.
- Marr, D. (1982) *Vision*. San Francisco: Freeman
- Mather, G. (1989) The role of subjective contours in capture of stereopsis. *Vision Res.* **29**, 143-146 (1989).

Paradiso, M.A., Shimojo, S. & Nakayama, K. (1989) Subjective contours, tilt aftereffect, and visual cortical organization. *Vision Res.* **29**, 1205-1213.

Parks, T.E. (1984) Illusory figures: A (mostly) atheoretical review. *Psychological Bulletin* **95**, 282-300.

Petersik, T.J., Hicks, K.I. & Pantle, A.J. (1978) Apparent movement of successively generated subjective figures. *Perception* **7**, 371-383.

Ramachandran, V.S. & Cavanagh, P. (1985) Subjective contours capture stereopsis. *Nature* **317**, 527-530.

Redies, C., Crook, J.M. & Creutzfeldt, O.D. (1986) Neural responses to borders with and without luminance gradients in cat visual cortex and dorsal lateral geniculate nucleus. *Exp. Brain Res.* **61**, 469-481.

Schuhmann, F. (1904) Einige Beobachtungen über die Zusammenfassung von Gesichtseindrücken zu Einheiten. *Psycholog. Studien* **1**, 1-32.

Sloane, M.E. (1985) Binocular rivalry: A psychophysics in search of a physiology. In: D. Rose & V.A. Dobson (Eds.), *Models of visual cortex*. Chichester: Wiley. (p 211-222)

Smith, A. & Over, R. (1975) Tilt aftereffect with subjective contours. *Nature* **257**, 581-582.

Ullman, S. (1976) Filling in the gaps: the shape of subjective contours and a model for their generation. *Biolog. Cybern.* **25**, 1-6.

Ullman, S. (1989) Aligning pictorial descriptions: an approach to object recognition. *Cognition* **32**, 193-254.

von der Heydt, R., Peterhans, E. & Baumgartner, G. (1984) Illusory contours and cortical neuron responses. *Science* **224**, 1260-1262.

von der Heydt, R., Peterhans, E. & Baumgartner, G. (1990) Neuronal processing of contours. *NIPS* **5**, 152-155.

Walker, J.T. & Shank, M.D. (1988) Interactions between real and subjective contours in the Bourdon illusion. *Perception & Psychophysics* **43**, 567-574.

Whitmore, C.L.G, Lawson, R.B. & Kozora, C.E. (1976) Subjective contours in stereoscopic space. *Perception Psychophys.* **19**, 211-213.

Wolfe, J.M. (1986) Stereopsis and binocular rivalry. *Psychol. Review* **93**, 269-282.

### **Acknowledgement**

We would like Norbert Welsch for discussions. Ellen Hildreth and Shimon Ullman made valuable comments on an earlier version of this paper. We thank Angelika Hildinger for help with the experiments. Marcia Ross for correcting the English, and all the subjects for their participation. Supported by the Deutsche Forschungsgemeinschaft (Heisenberg Programme).